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MIGRATION BEHAVIOR OF TUNDRA SWANS FROM THE YUKON-KUSKOKWIM DELTA, ALASKA

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ABSTRACT.—Tundra Swans (*Cygnus columbianus columbianus*) fitted with satellite transmitters (PTTs) on the outer coast of the Yukon-Kuskokwim (Y-K) Delta, Alaska, migrated eastward across the Y-K Delta in late September and stopped at wetlands on the west side of the Alaska Range during early October. After crossing the Alaska Range, swans stopped briefly on the Susitna Flats of Upper Cook Inlet. They then migrated eastward into the Yukon, Canada, and from there flew southward, paralleling the Wrangell Mountains through the interior of the Yukon to a staging area in northeastern British Columbia. They gradually migrated through central Alberta and southwest Saskatchewan and across Montana to a staging area in southeastern Idaho. They remained in southeastern Idaho from mid-November until early December when they migrated across Nevada to the Sacramento-San Joaquin Delta of California. Spring migration routes were similar to those used in autumn. Band returns and observations of neck-banded swans corroborated the general autumn and spring migration routes of PTT-marked birds. Swans stopped only briefly (<3 days) at staging areas in Alaska and northern Canada but lingered at migration areas in Alberta, Saskatchewan, and Idaho. *Received 23 Oct. 1996, accepted 15 April 1997.*

Despite their conspicuousness, we have a poor understanding of Tundra Swan (*Cygnus columbianus columbianus*) migration pathways. Information is particularly lacking from northern migration areas, especially for Tundra Swans originating from the Yukon-Kuskokwim (Y-K) Delta, the most important breeding area for the species in North America (Sladen 1973, Sladen and Kistchinski 1977, Bellrose 1980).

Swans from the Y-K Delta are part of the western population that nests in Alaska on coastal tundra habitat from Kotzebue Sound, south to Bristol Bay and Kodiak Island, and westward to Unimak Island on the Alaska Peninsula (Wilk 1988, Limpert et al. 1991, Spindler and Hall 1991). Swans from the western population winter in 12 Pacific Flyway states and the province of British Columbia, with most wintering in California (Sherwood 1960, Bellrose 1980, Paullin and Kridler 1988). It is unknown if swans from specific breeding areas within the western population have affinities for discrete wintering and staging areas.

Here we present results from a study that tracked the movements of

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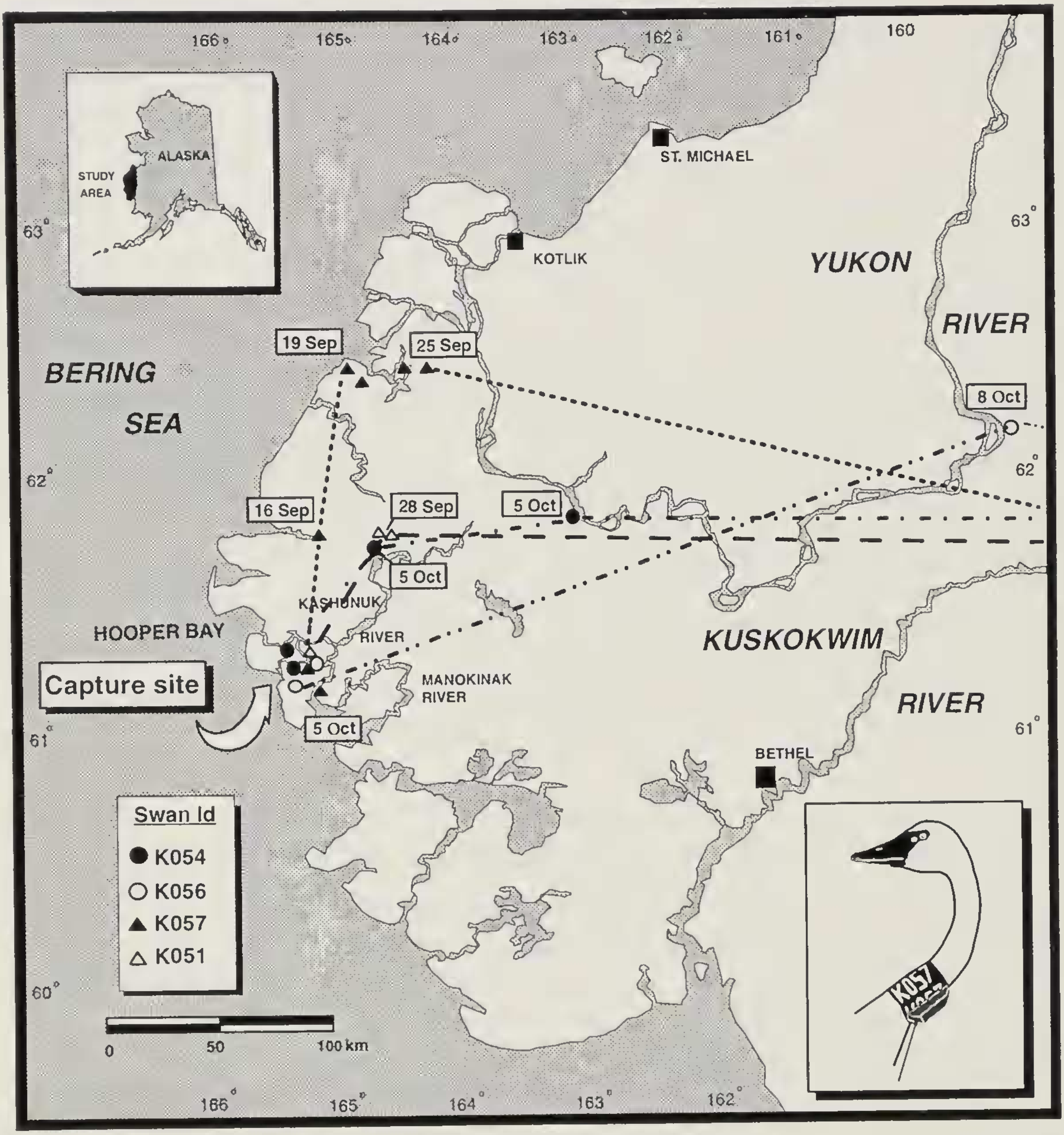

FIG. 1. Movements of four PTT-marked Tundra Swans during September and early October on the Yukon-Kuskokwim Delta, Alaska. in 1994. Inset—Tundra swan with satellite transmitter glued onto plastic neck band.

satellite-marked Tundra Swans during autumn and spring migration between the outer Y-K Delta and wintering areas in California. We compare our results with the distribution of observations of swans we neck-banded and with the recoveries of birds leg-banded on the Y-K Delta.

STUDY AREA AND METHODS

Seven females with cygnets and two males were captured and fitted with satellite transmitters (platform transmitting terminals, or PTTs) during August 1994 near Old Chevak (61°26′N, 165°27′W) on the outer Y-K Delta, Alaska (Fig. 1). We also captured flightless swans opportunistically during July and August 1987–1994 and fitted them with plastic coded neck bands (Sherwood 1966, Sladen 1973) and metal U. S. Fish and Wildlife Service leg bands. We used three types of PTTs, built by different manufacturers. The PTTs weighed 30–50 g, and were attached to the neck bands (Higuchi et al. 1991) using epoxy glue (Fig. 1—inset). PTTs were programmed to transmit every 90 s for 4–5 h and then stop transmitting for 43–44 h, thus allocating battery capacity over a longer period of tracking. Expected transmitter life was six months. PTT transmissions were collected by Service Argos (Landover, Maryland) receivers on board two National Oceanographic and Atmospheric Administration (NOAA) polar-orbiting environmental satellites (Fancy et al. 1988, Harris et al. 1990). For each satellite overflight that received two or more transmissions from a PTT, Service Argos calculated its location using the perceived Doppler shifts of the PTTs signal frequency together with satellite position data. The Doppler method of locational derivation resulted in two solutions that Service Argos reports as 'primary' and 'alternate'.

We subscribed to two data processing products offered by Service Argos: Standard Processing and Auxiliary Location Processing (formerly called 'Animal Tracking Service'). Standard Processing provided primary locations for PTTs when four or more signals were received during a satellite overflight and several data processing criteria were met (Argos 1996). Auxiliary Location Processing provided alternate locations for all Standard Processing locations, as well as primary and alternate locations for data that failed Standard Processing criteria, including satellite overflights that only recovered two or three PTT transmissions. Service Argos reported the accuracy of Standard Processing locations to be generally within 1 km, and that use of locational data from Auxiliary Location Processing was at the discretion of the investigator (Petersen et al. 1995).

We used a series of quantitative and qualitative criteria to remove aberrant locations that were typical of animal tracking databases which used the Argos 'Doppler' system (Fancy et al. 1988). We selected one location from each primary/alternate pair (or removed both locations from the database) by considering three factors; minimum travel distance from the previous location, rate of movement from the previous location, and/or locational redundancy with the previous or a subsequent location. Our approach was conservative in that we removed all locations lacking reasonable biological plausibility unless they were validated by subsequent locations in the vicinity.

We summarized distribution information from sightings of neck-banded birds obtained before May 1996 by volunteer observers that were reported either directly to us, to the U. S. Geological Survey Bird Banding Laboratory (BBL), or to state and federal biologists. Multiple observations of the same marked individual were included only if they differed by location, year, or season. We also summarized recoveries of swans leg-banded on the Y-K Delta and reported to the BBL before September 1995.

RESULTS

We obtained sufficient data to interpret the migratory patterns of four of the PTT-marked birds, all of which were adult females. We were unable to document the causes of PTT failure. Likely possibilities included: failure of batteries or electronic components, mechanical breakage of antenna or collar, or swan mortality. Mortality was ruled out for one swan whose PTT failed shortly after deployment but was observed in the Willamette Valley, Oregon, in November–December. Although PTTs were programmed to transmit location information every two days, none of the transmitters provided such information on a consistent basis.

Swans moved only short distances immediately after capture, as expected for adults with cygnets. PTT-marked swans remained near capture sites throughout August and most of September (Fig. 1). After the onset of migration in late September, some transmittered swans stopped along the Bering Sea coast or major rivers before continuing eastward across the Y-K Delta (Fig. 1).

After departing the Y-K Delta, swans used wetlands on the upper Kuskokwim River before crossing the Alaska Range and stopping on the Susitna Flats of Upper Cook Inlet (Fig. 2, site B; Table 1). They then migrated eastward across Alaska into the Yukon Territory and then southward, paralleling the Wrangell Mountains through the interior of the Yukon into northeastern British Columbia. Despite relatively mild autumn weather, swans stopped only briefly (<7 days) at staging areas in Alaska and Yukon Territory (Table 1). From northeastern British Columbia, swans migrated to central Alberta and southwest Saskatchewan where they remained for up to three weeks during late October and early November before flying across Montana to southeastern Idaho. They remained near the Snake River in southeastern Idaho from mid-November until early December when they migrated across Nevada to the Sacramento-San Joaquin Delta of California.

Two PTTs functioned longer than expected and provided location information throughout winter and during spring migration (Tables 1, 2). One swan (K056) wintered in both the Sacramento-San Joaquin Delta and the Sacramento Valley, moving between the two areas several times during December-February. The other swan (K054) remained in the Sacramento-San Joaquin Delta. The swans took different spring migration routes: K056 migrated north through Oregon and Idaho to Alberta, while K054 flew east to Utah before continuing north into Montana (Fig. 3, Table 2). Although the two swans used different routes, the timing of migration was similar. Both departed California in late February and arrived in Idaho and Montana the third week of March.

Our estimates of the maximum rate-of-movement ranged from 60–90 kph (N = 12). To reduce the influence of location error on estimates of distance travelled between locations, we restricted our analysis of rate-of-movement to instances when ≥30 min expired between consecutive locations and/or the distance travelled was ≥50 km. The majority (N = 9) of our maximum estimates were obtained from three birds migrating during 13–18 October from eastern Alaska to British Columbia and Alberta, where satellite coverage was still optimum (Fancy et al. 1988).

The general route of migrating swans (Figs. 2, 3) was corroborated by

TABLE 1

AUTUMN MIGRATION AND WINTERING AREAS USED BY TUNDRA SWANS MARKED WITH SATELLITE TRANSMITTERS ON THE YUKON-KUSKOKWIM DELTA, ALASKA IN 1994

Map reference[a]	State/Province	Geographic location	Coordinates		Swan Id.	Location		No. locs[b]
			Lat.	Long.		First	Last	
A	Alaska	W. side of Alaska Range	61.347	154.615	K054	7 Oct	7 Oct	1
		Stony River	61.606	154.657	K056	9 Oct	9 Oct	1
		S. Kuskokwim	62.649	153.860	K051	10 Oct	10 Oct	1
B	Alaska	Cook Inlet	61.287	150.255	K054	10 Oct	10 Oct	1
			61.235	150.266	K056	12 Oct	13 Oct	2
C	Alaska	Tetlin	62.614	142.077	K056	14 Oct	15 Oct	1
D	Yukon	NE Kluane	61.812	137.378	K051	12 Oct	12 Oct	1
E	Yukon	Watson Lk.	60.454	125.411	K054	13 Oct	14 Oct	4
F	British Columbia	Ft. Nelson/ Liard River	58.201	122.778	K051	16 Oct[b]	16 Oct	1
			59.186	123.919	K054	14 Oct	18 Oct	4
G	Alberta	Battle River Area (150 km SE Edmonton)	52.676	112.150	K054	22 Oct	24 Oct	4
			52.375	111.608	K056	22 Oct	28 Oct	7
			52.446	110.804	K057	10 Oct	16 Oct	6
H	Saskatchewan	Southwest	49.253	109.233	K057	22 Oct	2 Nov	6
			49.847	109.175	K054	30 Oct	30 Oct	1
I	Idaho	Snake River (Southeast)	43.066	112.704	K054	12 Nov	5 Dec	10
			43.167	112.924	K056	15 Nov	4 Dec	7
J	Nevada	Ruby Lake Northeast	40.309	115.906	K057	10 Nov[c]	10 Nov	1
			41.448	117.080	K054	11 Dec	11 Dec	1
K	California	Sacramento–San Joaquin Delta	38.152	121.547	K054	22 Dec	9 Feb	51
			38.417	121.653	K056	6 Jan[d]	9 Feb	12
L	California	Sacramento Valley	39.401	121.755	K056	27 Dec	17 Feb	5

[a] See Fig. 2.
[b] Number of locations in the vicinity; usually only one "fix" at the exact coordinates. Locations based on only one set of coordinates may have been birds in flight.
[c] Last location information for this PTT.
[d] K056 moved several times between areas K and L from late December through mid-February.

TABLE 2

SPRING MIGRATION AREAS USED BY TUNDRA SWANS MARKED WITH SATELLITE TRANSMITTERS ON THE YUKON-KUSKOKWIM DELTA, ALASKA IN 1994

Map reference[a]	State/ Province	Geographic location	Coordinates		Swan Id.	Location		No. locs[b]
			Lat.	Long.		First	Last	
M	Oregon	Klamath Marsh	42.903	121.644	K056	28 Feb	18 Mar	5
m	Utah	Salt Lake	41.534	112.094	K054	27 Feb	3 Mar	2
n	Montana	Freezeout Lake	47.665	112.141	K054	19 Mar	19 Mar	1
N	Idaho	Coeur d'Alene	47.305	116.506	K056	20 Mar	24 Mar	2
o	Alberta	Milk River	49.121	110.474	K054	14 Apr	20 Apr	3
O	Alberta	Vauxhall–SE Calgary	50.147	112.329	K056	2 Apr	2 Apr	1
p	Montana	Cut Bank	48.718	112.157	K054	22 Apr	10 May[c]	2
P	Alberta	Red Deer River[d]	51.876	113.052	K056	6 Apr	16 Apr	9
Q	Alberta	Lesser Slave Lk.	55.425	115.430	K056	18 Apr	18 Apr	2
R	Alberta	Peace River	55.885	118.096	K056	22 Apr	26 Apr	3
S	Yukon	Teslin Lake	60.245	132.605	K056	27 Apr	27 Apr	1
T	Alaska	Tetlin	62.908	141.631	K056	29 Apr	29 Apr	5
U	Alaska	Holy Cross	62.114	159.818	K056	1 May[c]	1 May	2

[a] See Fig. 3.
[b] Number of locations in the vicinity; usually only one "fix" at the exact coordinates. Locations based on only one set of coordinates may have been birds in flight.
[c] Last location information for this PTT.
[d] Range of latitude 51.105–51.876 and longitude 112.758–113.530.

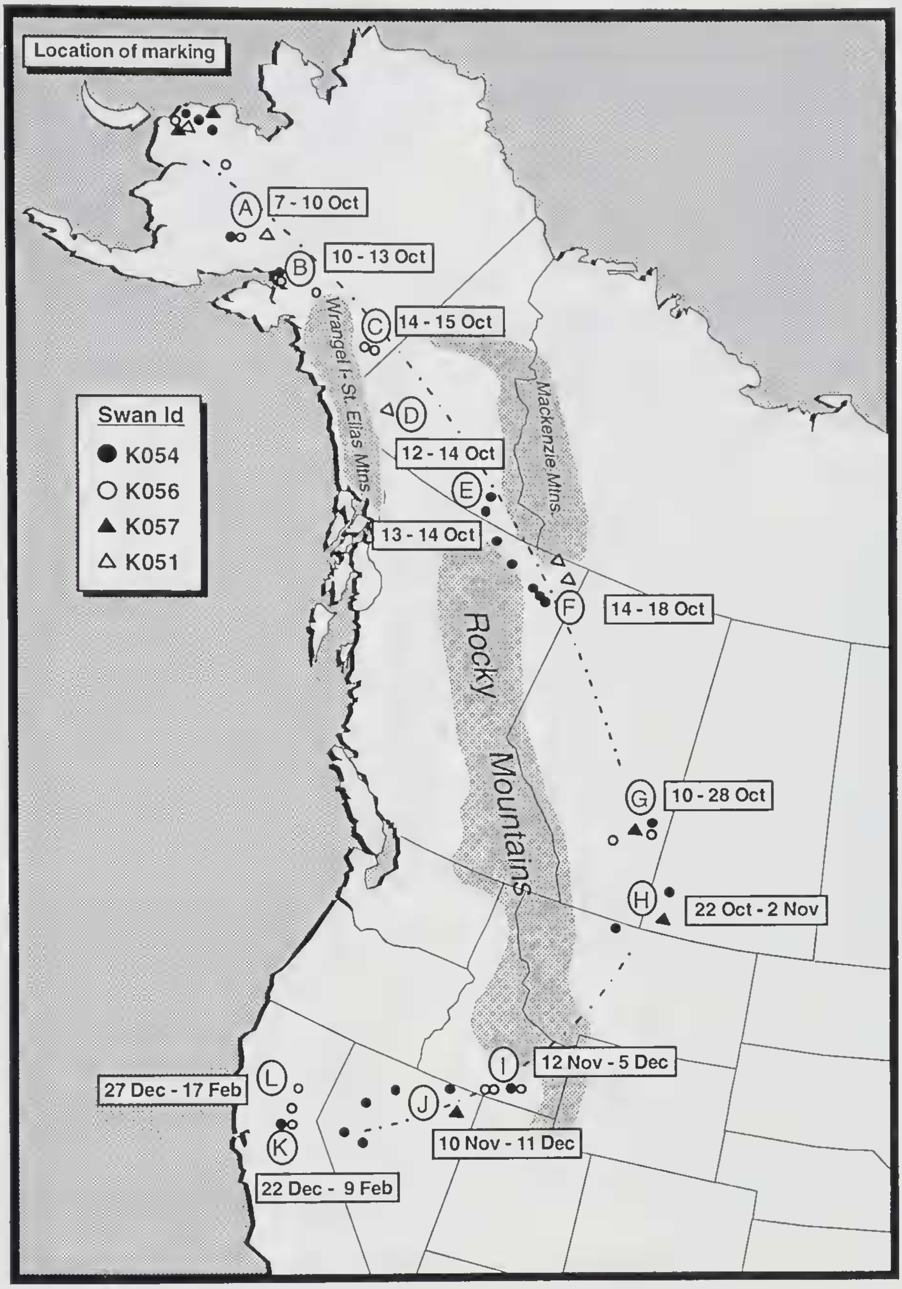

FIG. 2. Autumn migration route of four PTT-marked Tundra Swans from their breeding grounds on the Yukon-Kuskokwim Delta, Alaska to their wintering grounds in California. Letters refer to locations described in Table 1.

regional biologists that noted flocks of swans in many of the geographic areas used by PTT-marked birds. The distribution of recoveries of leg-banded swans and observations of neck-banded swans from the Y-K Delta differed slightly from the distribution of locations of PTT-marked birds (Fig. 4). Seventeen percent (16 of 92) of the observations and recoveries were in northern Utah whereas only one PTT-marked bird visited this

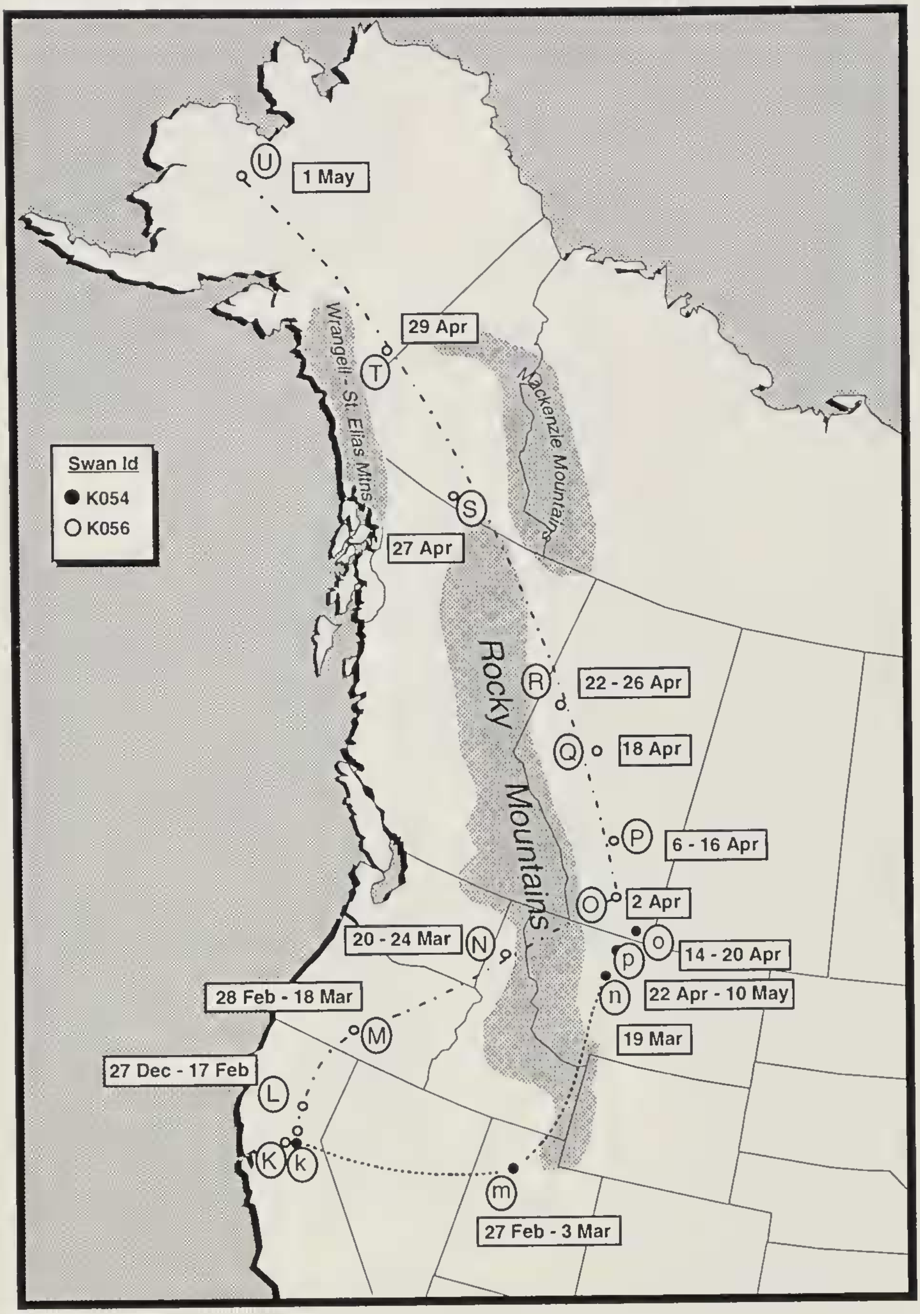

FIG. 3. Spring migration routes of two PTT-marked Tundra Swans from their wintering grounds in California to their breeding ground on the Yukon-Kuskokwim Delta, Alaska. Letters refer to locations described in Table 2.

area. Similarly, nearly 12% (11 of 92) of the recoveries and observations of swans were in Oregon, Washington, or southwestern British Columbia. None of our swans with functioning transmitters visited these areas, although one swan with a failed PTT was observed in November and December in northwestern Oregon. In contrast, the PTT-marked swans used many areas in Canada and Alaska for which there was very little if any observation or recovery data.

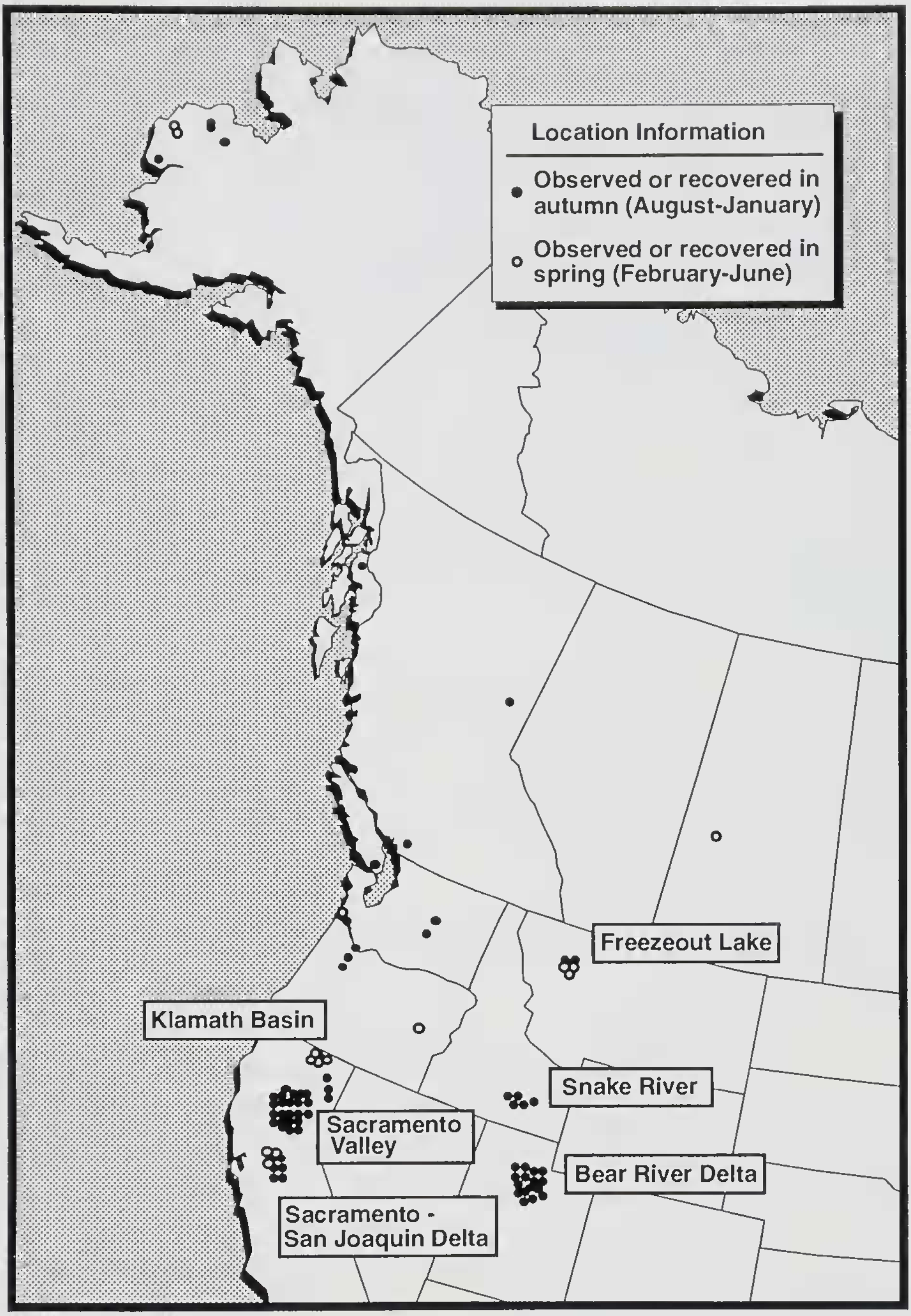

FIG. 4. Distribution of observations and recoveries of leg-banded (N = 46) and neck-banded (N = 46) Tundra Swans from the Yukon-Kuskokwim Delta, Alaska. Does not include one direct recovery in Georgia and one direct recovery in Texas.

Resightings of neck-banded swans at more than one location during the same year provided additional information on migration routes. A neck-banded pair was observed at Freezeout Lake, Montana, in late October and subsequently observed on the Bear River Delta of Utah in early December. Another swan observed in the Sacramento Valley in late January was seen at Freezeout Lake in late February.

DISCUSSION

Tundra Swans on the Y-K Delta generally do not fledge until September, and some not until October (Lensink 1973). Hence, it is not surprising that PTT-marked swans, all of which were with young, generally remained near marking locations through September. Swans likely undertook local movements during late September and early October (Fig. 1) to join other swans prior to autumn migration (Kear 1972).

Several different migration routes have been proposed for the western population of Tundra Swans, based largely on surveys and a few band recoveries. Sladen (1973) and Bellrose (1980) indicate three possible pathways are used: (1) Coastal route from south central Alaska, along British Columbia to Washington; (2) British Columbia route from central Alaska through interior British Columbia to Washington; and (3) Trans-Rocky Mountain route, similar to what we have reported here, but originating in eastern Alaska.

Our PTT-marked swans did not migrate via a coastal route or through interior British Columbia. The only evidence of the use of a coastal route by Y-K Delta swans, is a single recovery of a leg-banded swan in southeast Alaska (Fig. 4). The coastal route is most likely used by Tundra Swans from the Alaska Peninsula and Bristol Bay (Bellrose 1980). Recoveries and observations of swans in Washington and British Columbia (Fig. 4) indicate some Y-K Delta swans migrate via the interior British Columbia route.

PTT-marked swans used a trans-Rocky Mountain route during autumn and spring migrations. This general migratory pathway is thought to be the most commonly used, with some variations concerning specific portions of the route (Sherwood 1960, Bellrose 1980, Pacific Flyway Study Committee 1983, Paullin and Kridler 1988). Our data showed no use of Lake Athabasca in northeastern Alberta, considered by Bellrose (1980) to be an important autumn staging area for Tundra Swans from western Alaska. It may be that western population swans do not stop there (e.g., Sladen 1973, but see Limpert et al. 1991), that it is used by western swans from other nesting areas, or that we had too few PTT-marked birds to determine the importance of the area to Y-K Delta swans. Bellrose (1980) thought interior-migrating swans followed two corridors after arriving in Alberta; one equivalent to the route taken by our PTT-marked swans through western Montana, and the other a path across northern Idaho to eastern Oregon and south to the Klamath Basin of California.

Paullin and Kridler (1988) also reported autumn movements of swans from eastern Oregon to the Klamath Basin, and to the Willamette Valley of western Oregon. The latter pathway may have been the route taken by one of our swans with a non-functioning PTT observed in the Willamette Valley, Oregon in early November (M. Naughton, pers. comm.).

During spring, the two different trans-Rocky Mountain routes used by the PTT-marked swans (Fig. 3) were similar to pathways reported for dye-marked swans of unknown breeding origin marked in eastern Oregon (Paullin and Kridler 1988). Northern Idaho and Utah are well known as important spring staging areas for Tundra Swans (Bellrose 1980).

Relocations of our PTT-marked and neck-banded swans showed no indication of birds using migration or staging areas of the eastern population (all Tundra Swans breeding north and east of Kotzebue Sound, and wintering along the Atlantic Coast—Limpert et al. 1991). However, two of 92 (2%) swans leg-banded on the Y-K Delta were recovered from migration and wintering areas of the eastern population. Strong fidelity to migration and wintering areas was also reported by Limpert et al. (1991), who found only one of 25 (4%) Tundra Swans neck-banded on the Y-K Delta outside the normal migration and wintering areas of the Western Population. Mixing of swans from the eastern and western populations is thought to occur at staging areas near Lake Athabasca, Alberta (Bellrose 1980, Limpert et al. 1991), the MacKenzie Delta (Paullin and Kridler 1988) and also at Freezeout Lake, Montana (M. Schwitters, pers. comm.).

Tundra swans cygnets are among the slowest of northern waterfowl to grow (Bellrose 1980), and they fledge at a smaller proportion of adult mass than geese (Sedinger 1992). Tundra Swans on the Y-K Delta become volant nearly three weeks after sympatric nesting Cackling Canada Geese (*Branta canadensis minima*) and Greater White-fronted Geese (*Anser albifrons frontalis*), but all three species generally begin autumn migration in late September or early October (Lensink 1973; C. Ely, unpubl. data). Cygnets are thus developmentally less mature than goslings at the beginning of migration and are likely less able to sustain long, uninterrupted flights. It was thus not unexpected that swans made many stops to rest and replenish body reserves during autumn migration. We were surprised however, that swans remained so briefly at northern areas, and did not stop to stage for more than a few days, until they reached central Alberta. Swans have generally been reported to be able to remain longer than geese at northern breeding and staging areas due to the thermoregulatory benefits of large body size and the greater availability of aquatic compared to terrestrial foods after autumn snowfall. However, newly fledged cygnets are much smaller than adult swans, and young accompanied by their parents are often the first to arrive on wintering areas (Kear 1972).

We were only able to monitor PTT-marked swans for one year, but there is evidence of annual variation in timing and use of migration areas.

One PTT-marked swan (K056) that was in southeastern Idaho from 15 November through 4 December 1994 and then on the Sacramento-San Joaquin Delta on 27 December 1994 (Table 1), was observed in the Klamath Basin of northeastern California on 30 November 1995. It is evident that K056 completed migration earlier in 1995 than 1994. K056 may also have altered its migration route between years. Alternatively, K056 may have migrated through the Klamath Basin in early December 1994 before arriving in the Sacramento-San Joaquin Delta.

Our estimate of a maximum speed of migration of 60–90 kph was less than the maximum flight speed of 135 kph speed reported for a Tundra Swan tracked during spring migration with conventional (VHF) telemetry (Alerstam 1990:242). It was, however, similar to the 73 kph ground speed reported by Sladen and Cochran (1969) for a VHF radio-marked juvenile Tundra Swan tracked during spring migration. Flight speeds of swans are highly variable due in part to the presence of head and tail winds associated with weather systems (Ogilvie 1972). Also, flight speeds might be greater in spring (e.g., Alerstam 1990) when adults are not accompanied by young.

Tundra Swans are one of the largest species of flying birds, and one of the first species of birds to be fitted with satellite transmitters. Satellite transmitters have been successfully used to track Bewick's Swans (*Cygnus c. bewickii*) during spring migration in Europe (Nowak 1990) and Asia (Higuchi et al. 1991), where the main objective was to locate the breeding areas of birds marked during winter. Satellite transmitters used on birds are generally smaller and have less battery capacity and are configured to transmit with less signal strength compared to PTTs typically used on large terrestrial mammals (see Caccamise and Hedin [1985] for review of avian transmitter loads). As a result, location information obtained from small avian PTTs is often only accurate to within a few kilometers (Ely et al. 1993, Petersen et al. 1995). Fortunately for studies of species undergoing long migrations, the magnitude of location error is generally negligible relative to the length of the migration route.

Spurious results are always possible when relying on small samples of experimental birds to determine behavior patterns. There is also a degree of subjectivity involved in choosing the "best" set of possible coordinants from the Argos processing system (Fancy et al. 1988). When possible, we tried to verify the use of specific staging areas with visual observations. Verification of southern staging areas was also provided by observations of neck-banded swans and recovery information from leg-banded birds.

Neck band observations and band recovery information (Fig. 4) complemented the PTT data. Banding data provided distribution information on many nearly non-experimental (leg band only) swans over a period of years, but was somewhat misleading because of both temporal and geographic biases in recovery probabilities. In contrast, PTT data were restricted to a few individuals over a relatively short time period, but were not biased by the distribution of observer (or hunter) effort. The latter is an important consideration for Tundra Swans as recoveries and observations are more common in heavily populated areas, especially where there is a sport harvest such as in Utah.

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